A survey method for evaluating drought-sensitive bryophytes in fragmented forests: A bryophyte life-form based approach

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Title: A survey method for evaluating drought-sensitive bryophytes in fragmented forests: a bryophyte life-form based approach

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Abstract

Drought-sensitive bryophytes are especially vulnerable to edge effects caused by forest fragmentation. Because of increased forest fragmentation, these bryophyte species are declining and are in need of conservation. Considering that a field survey including all bryophyte species is very time consuming, methods that make identification less difficult should be tested for their usefulness in conservation. This paper describes an alternative survey method that utilizes the correlation between bryophyte life-forms and microclimates for evaluating drought-sensitive bryophytes. This survey method was examined using epiphytic bryophyte flora on tree trunks in 27 fragmented forests of Kyoto city, in the western part of Japan. The usefulness of life-forms for this evaluation was discussed based on the correlation of life-forms with species richness and microclimates. The results indicated that, while life-from richness was considered to reflect the heterogeneity of moisture availability and light intensity in bryophyte habitats, a certain life-form category (for example, fans and dendroids) seemed to correlate with drought sensitivity of bryophytes. Considering this correlation, an alternative survey method was proposed that utilizes the richness of hygrophilous life-forms. This survey method seems to be more cost-effective than a traditional all-species

survey, and provides an important step toward the conservation of drought-sensitive species.

Keywords

edge effect, forest interior, hygrophilous life-form, life-form richness, moisture availability

1. Introduction

Drought-sensitive species are often the most vulnerable bryophyte species in a forest (Gignac and Dale, 2005; Hylander et al., 2005; Baldwin and Bradfield, 2007). Fragmented forest stands are smaller units compared to continuous forest stands (Murcia, 1995). These are affected more by edge effects from the surrounding open landscape (drier microclimate) than are large continuous forests (Matlack, 1993; Murcia, 1995). This environmental change caused by edge effects has a serious negative impact on drought-sensitive bryophytes (Acebey et al., 2003; Gignac and Dale, 2005; Hylander et al., 2005; Baldwin and Bradfield, 2007). Because of increased forest fragmentation (Saunders et al., 1991; Debinski and Holt, 2000), these bryophyte species are declining and are in need of conservation.

How do we know that drought-sensitive bryophyte species still occur in a fragmented forest stand? What kind of survey can be done? Since a field survey including all

bryophyte species is very time consuming, and since some species are very hard to identify, methods that make identification less difficult should be tested.

Bryophyte life-forms were focused on as a key indicator of drought-sensitive species in fragmented forests. Bryophyte life-forms are a higher level of organization compared to bryophyte growth-forms which are based on the morphological characteristics of bryophytes (Bates, 1998). That is, life-forms combine the features of the growth-forms with the assembly of shoots into colonies, and modification of the resultant form by local environmental conditions (Bates, 1998). As a consequence, the life-forms significantly interact with bryophyte habitat conditions. Some species even modify their life-forms according to environmental conditions (Birse, 1957). Therefore, the life-forms seem to be useful for evaluating habitat conditions important for drought-sensitive species. Furthermore, since life-forms can be recognized at first glance in the field, they are easy to survey. Taking these useful advantages of life-forms into account, it may be helpful to test an alternative survey method for evaluating drought-sensitive species based on their life-forms.

Described herein is an alternative survey method for evaluating drought-sensitive bryophytes, which utilizes the correlation between their life-forms and the microclimate. Since the results of this work indicated that certain life-form categories (for example fans and dendroids) and drought sensitivity of bryophytes appear to be correlated, it is suggested that field surveys of bryophyte species can use these life-form categories to represent drought-sensitive bryophyte species. This survey method seems to be more cost-effective than a traditional all-species survey, and can contribute to the conservation of drought-sensitive bryophytes.

2. Methods

2.1. Study area

All of the study sites were located in Kyoto city (34° 59′ N, 135° 44′ E), Kyoto Prefecture, Japan (Fig. 1). Kyoto is an inland city, making up part of the northern half of the Kyoto (Yamashiro) Basin. In the Kyoto Basin differences in temperature between summer and winter are large. Mean monthly temperatures range from 8.9 °C in January to 23.9 °C in August and the average annual precipitation is 1545 mm (National Astronomy Observatory, 2007).

Twenty-seven fragmented forests in the Kyoto Basin were selected as study sites (Fig. 1). All sites were matched for climate and geology; these fragmented forests were isolated from continuous forests more than 35 years ago (Murakami and Morimoto, 2000). The study sites were small (0.13-60.27 ha, mean; 5.95 ha) and were

surrounded by artificial patches such as buildings and roads. The main tree species in the study sites were *Cinnamomum camphora* L. Nees and Eberm. and *Quercus glauca* Thunb.; often *Celtis sinensis* Pers. var. *japonica* (Planch.) Nakai. or *Aphananthe aspera* (Thunb.) Planch. were found in the lowland forests, and *Quercus serrata* Thunb. or *Pinus densiflora* Sieb. et Zucc. were found in the hilly forests.

[Place Fig. 1 about here]

2.2. Bryophyte sampling

In this study, the epiphytic bryophyte flora on tree trunks was employed to examine and evaluate the alternative survey method. The study sites were completely surveyed thrice from February in 2006 to January in 2007 in order to ensure that small species were not overlooked. Bryophyte flora on all tree trunks, except for those covered with soil, was investigated, and the epiphytic bryophytes on the lower 2.0 m of the tree

153 trunks, including the roots, were sampled. These species are crucial for the purpose of
154 conservation in fragmented forests for the following two reasons. First, bryophytes tend
155 to dominate in humid microhabitats; and therefore, epiphytic bryophytes make a
156 significant contribution to the species richness and biomass on the lower part of the
157 trunk (Hale, 1952; Iwatsuki, 1960; Hoffman, 1971). Second, bryophytes growing on
158 tree bases are vulnerable to desiccation (Fuertes et al., 1996), and can be expected to be
159 damaged heavily by edge effects.
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162 Using the sampling method described above, the presence-absence of all epiphytic
163 bryophyte species and life-forms was recorded for each study site. The presence of
164 the life-forms was directly established in the field. Recorded bryophytes only
165 identified to the genus-level were not included in calculations of species richness if
166 any species of that genus was identified separately on the site. All collected
167 bryophytes were preserved and returned to the laboratory for identification. The
168 nomenclature followed Iwatsuki (2001, 2002). Bryophyte life-forms in this study
169 followed those described by Bates (1998).
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173 **2.3. Modelling methods**

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176 First, the correlation of life-forms with species richness and microclimates was
177 examined using a multiple linear regression model (linear model) and a regression tree
178 model (tree model) (Breiman et al., 1984; De'ath and Fabricius, 2000). In the
179 modelling, epiphytic bryophyte species richness was used as a dependent variable,
180 whereas life-form richness and presence/absence of each life-form were explanatory
181 variables. Based on these results, the usefulness of life-forms for representing
182 drought-sensitive species was examined, and how the life-forms should be utilized to
183 evaluate these species was discussed.

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186 To clarify the usefulness of life-forms for representing drought-sensitive species,
187 linear and tree models were also built based on environmental conditions. Then these
188 results were used in comparison with those of the life-forms. In this model, the

following 10 environmental conditions in each study site were used as explanatory variables: patch size (hectares), perimeter of patch (m), highest elevation (m), lowest elevation (m), elevation range (m), distance from the nearest patch (km), distance from the surrounding mountains (km), percent of canopy cover (%), forest management practice (managed or unmanaged), and the presence/absence of streams or ponds. The measurements of these environmental variables were taken from aerial photographs (photos taken by the Geographical Survey Institute in 2000) and the city planning map of Kyoto City (1:2500; surveyed by Kyoto municipal government office in 1993). The types of forest management practices and the presence/absence of streams or ponds were based on field observations. Before the linear model analysis, patch size was logarithmically transformed and the percent of canopy cover was arcsine-transformed to reduce heteroscedasticity.

2.4. Development of the linear and tree models

Linear and tree models have been widely demonstrated to have great utility in predicting species-environment relationships (Kerns and Ohmann, 2004; Pittman et al., 2007). Linear models are an extensively tested and widely understood technique that has often performed well in modelling ecological relationships. However, linear models are limited to a global linear fit and have assumptions of normality and homoscedasticity in the explanatory data (Guisan and Zimmermann, 2000). In contrast, tree models are ideal for capturing relationships that make sense ecologically, but are difficult to reconcile with conventional linear models (De'ath and Fabricius, 2000). Therefore, tree models are often preferred for modelling species richness and abundance (De'ath and Fabricius, 2000; Dumortier et al., 2002; Kerns and Ohmann, 2004; Pittman et al., 2007). Tree models are constructed by binary recursive partitioning of data into homogeneous subgroups defined by dependent variables (Breiman et al., 1984). Homogeneity is determined by impurity, which is an indicator that measures the similarity of subgroups (Breiman et al., 1984). The process of partitioning continues until stopping criteria (variously defined) are met (Breiman et al., 1984). The resultant model is usually overly large. Therefore, a pruning method is applied to trim it back to the size in which the splits significantly reduce variability within subgroups (Breiman et al., 1984). The cross-validation procedure according to

a pruning rule gives an estimate of the pruning level needed to select a particular model that appears the most stable and valid (Breiman et al., 1984).

Linear and tree models were developed using the following procedure. In the development of the linear models, forward stepwise selection (0.05 alpha-to-enter and 0.10 alpha-to-remove) was used to select the important explanatory variables. The tree models were developed using the sums of squares about the group means for impurity, and the one standard error rule as the pruning rule (Breiman et al., 1984). The final optimum model size was selected using a ten-fold cross-validation. This procedure was repeated 50 times, and the most frequently occurring tree size was selected from the overall distribution of selected tree sizes because the optimum model size suggested from cross-validation will vary for each run (De'ath and Fabricius, 2000). Furthermore, explanatory variables in the tree models were deleted stepwise from the candidate models when masking effects were evident from strong competitor and surrogate splits (De'ath and Fabricus, 2000). Comparison of the tree models was based on proportional reduction in deviance (PRD), which roughly corresponds to the multiple coefficient of

242 determination (De'ath and Fabricus, 2000). All data were analyzed using R, a language
243 and environment for statistical computing (R Development Core Team, 2008).
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247 **2.5. Generality of the linear and tree models**
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250 The generality of the linear and tree models that were developed was tested through
251 their application to other fragmented forests in the Kinki district, in western Japan (18
252 sites). The same suite of model performance measures was used to evaluate generality.
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3. Results

3.1. Bryophyte flora survey

To determine epiphytic bryophyte species richness and the life-forms that were present, epiphytic bryophyte flora was surveyed on the lower 2.0 m of the trunks in the study sites. Across the study sites, a total of 98 species (67 moss and 31 liverwort species) were found (Table 1). In the 27 study sites, species richness ranged from a low of 10 species to a high of 63 species (mean = 32.3, SD = 14.0). As for life-forms, a total of 10 types were recorded (Table 1). Life-form richness ranged from a low of three types, to a high of nine types (mean = 6.5, SD = 1.8). These data were used in the following analysis.

[Place Table 1 about here]

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279 **3.2. Results of the linear and tree models**

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282 To determine the level of correlation between life-forms and species richness, the first
283 effort involved developing linear and tree models based on life-forms or environmental
284 conditions. In the linear model based on life-forms, only the life-form richness was
285 selected as a significant explanatory variable with a stepwise process ($y = 6.81x - 11.4$,
286 $R^2 = 0.731$, n = 27, $P < 0.01$: Fig. 2). Similarly, the linear model based on
287 environmental conditions selected only patch size from 10 types of candidate variables
288 ($y = 17.1x + 28.1$, $R^2 = 0.661$, n = 27, $P < 0.01$: Fig. 2). As for the tree models, the
289 resultant tree model based on life-forms contained six terminal nodes (Node A-Node F)
290 with five predictor variables (PRD = 0.817: Table 2, Fig. 3). These five predictor
291 variables were the presence/absence of fans, dendroids, thalloid mats, wefts, and short
292 turfs. The highest species richness was found in Node A in which both fans and
293 dendroids were found, whereas that of the lowest was in Node F without fans and wefts.
294 In contrast to this model, the tree model based on environmental conditions had only
295 two terminal nodes (Node G, F) with one split using patch size (PRD = 0.617: Table 2,

296 Fig. 3). The richness of epiphytic bryophyte species was higher in sites with a patch
297 size larger than 5.1 ha.
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300 [Place Figs. 2 and 3 and Table 2 about here]
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303 To test the generality of the results, these final linear and tree models were applied to
304 other fragmented forests in the Kinki district. This application produced results that
305 were similar to those of the 27 fragmented forests. That is, the linear and tree models
306 using life-forms had better predictive power (R^2 = 0.845; PRD = 0.750) than those using
307 environmental conditions (R^2 = 0.572; PRD = 0.511) for explaining epiphytic bryophyte
308 species richness. In addition, the presence of fans and dendroids was a good indication
309 of the highest species richness in these fragmented forests, whereas the absence of fans
310 and wefts was a good indication of the lowest species richness.
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These results indicated that the linear and tree models based on life-forms had better predictive power than those based on the measured environmental conditions. It is noteworthy that the explanatory variables selected in the linear model and the tree model were different in the evaluation models based on life-forms.

4. Discussion

The results of this study indicate that life-forms were more useful for explaining epiphytic bryophyte species richness than were the measured environmental conditions. They also indicate that the criteria for explaining species richness were different between the linear model based on life-forms and that of the tree model, because these models have different explanatory variables. These results provide some important insights for describing the alternative survey method proposed here, which can evaluate the diversity of drought-sensitive species.

4.1. Comparison of life-forms with environmental conditions

In the first stage of the investigation, the usefulness of bryophyte life-forms for representing drought-sensitive species was established thorough comparison with the

use of measured environmental conditions. Results showed that both the linear and tree models based on life-forms were more useful in explaining species richness than those based on measured environmental conditions. Among the environmental conditions, only patch size was selected as an explanatory variable. It is suggested that the usefulness of the models based on life-forms was due to the direct association of life-forms with bryophyte habitat conditions. Moisture availability and light intensity are important factors for bryophyte growth (Bates, 1998). Life-forms are usually interpreted as an adaptation to these microclimatic conditions, therefore, they are directly and strongly associated with those conditions (Bates, 1998). On the other hand, patch size is not directly but indirectly associated with these microclimates through edge effects and habitat heterogeneity (Gignac and Dale, 2005; Baldwin and Bradfield, 2007). Compared to the direct associations of life-forms, this indirect association of patch size cannot effectively reflect variations of these microclimatic conditions affected by factors other than patch size (e.g., canopy structures, degree of management, and bark conditions). Thus, life-forms seemed to be more suitable for evaluating species richness than was patch size in cases in which the species are strongly influenced by microclimates. Considering the fact that drought-sensitive species are

366 especially vulnerable to edge effects (Gignac and Dale, 2005; Hylander et al., 2005;
367 Baldwin and Bradfield, 2007), life-forms can be useful for representing these species.
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370 As for the usefulness of models based on environmental variables, one should take into
371 consideration the fact that the efficacy of these models in explaining species richness
372 largely depends on the measured environmental conditions. That is if microclimates,
373 such as humidity on trunks, are used in the model, this model may be more useful than
374 those based on life-forms. However, this kind of model is not suitable for practical use
375 since measuring microclimates is generally fairly elaborate (León-Vargas et al., 2006).
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379 **4.2. Linear model for representing drought-sensitive species**
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382 In the next stage of the investigation, linear models were used to reveal the correlation
383 between life-forms and drought-sensitive species. Results of the linear model based on

life-forms showed that the fragmented forests with higher species richness were characterized by higher life-form richness. This result might be explained by the strong correlation of each life-form with certain microclimatic conditions (Bates, 1998). Considering this strong correlation, the increasing heterogeneity of these microclimatic conditions leads to an increase in the richness of life-forms and of species. These correlations indicate that life-form richness can be useful for evaluating species richness correlated with heterogeneity of moisture availability and light intensity.

In addition to heterogeneity, high life-form richness seems to partially correlate with forest interior conditions characterized by relatively high moisture levels (Matlack,1993; Murcia, 1995, Gignac and Dale, 2005) . Since small fragmented forests are sometimes completely constituted by edge environments (Matlack, 1993), the presence of a forest interior is considered to be one of the key factors for increasing both the high heterogeneity of moisture availability and the occurrence of drought-sensitive species. Therefore, high life-form richness is likely to represent the drought-sensitive species that are related to the presence of a forest interior.

4.3. Tree model for representing drought-sensitive species

In the third stage of the investigation, tree models were employed to reveal the correlation between life-forms and drought-sensitive species. Results showed that fragmented forests with the highest species richness were characterized by the presence of fans and dendroids (Node A), and those with the lowest species richness, by the absence of fans and wefts (Node F). These results might be explained by the correlation between hygrophilous life-form richness and species richness. The life-forms characterizing Node A and Node F (fans, dendroids, and wefts) are hygrophilous (Bates, 1998), that is, they are relatively intolerant of desiccation. Therefore, they are expected to be much better adapted to living in the forest interior, where drought by edge effects (e.g., degree of desiccation of the shoots, length of the desiccation period) is less severe (Matlack, 1993; Murcia, 1995; Gignac and Dale, 2005). Given that bryophytes are prominent in humid habitats (Hoffman, 1971), it seems reasonable that several hygrophilous life-forms were associated with the highest species richness (Node A), and

420 also that the absence of these life-forms was associated with the lowest species richness
421 (Node F). Thus, since hygrophilous life-forms seem to correlate with the drought
422 sensitivity of bryophytes, they can be a useful representative of drought-sensitive
423 species. Furthermore, results obtained using the tree models suggest that the richness of
424 hygrophilous life-forms can be correlated with the richness of drought-sensitive species.
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427 The results of the tree model based on life-forms also indicated that thalloid mats and
428 short turfs were also principal determinants of epiphytic bryophyte species richness (Fig.
429 3). However, one must be careful in associating these two life-forms with drought-
430 sensitive species. The limitation of tree models is that they may not extrapolate well
431 across space or time because of their empirical nature (Kerns and Ohmann, 2004).
432 Therefore, to generalize the results of tree models we need a satisfactory explanation
433 with regard to selection of the predictive variables in the tree models. As for the two
434 life-forms, considering their weak association with humidity (Bates, 1998), it was not
435 fully explained why these life-forms could be an indicator of species richness based on
436 the theory of forest fragmentation. Given the empirical nature of tree models, the
437 selections of these life-forms are considered to be influenced by some site-specific

438 factors such as the differences in number or frequency of species assigned to the
439 different life-forms.
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443 **4.4. Survey method for evaluating drought-sensitive species**
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446 In the final stage of the investigation, an alternative survey method was explored for
447 evaluating the drought-sensitive species in fragmented forests, which is described below.
448 In the above discussion, the usefulness of the life-form richness of both total and
449 hygrophilous species for representing drought-sensitive species was determined.
450 Among the two life-form richness types, it is suggested that richness of hygrophilous
451 life-forms is suitable for evaluating the richness of drought-sensitive species because
452 this life-form richness directly correlates with the drought sensitivity of these
453 bryophytes. Therefore, this alternative survey method for evaluating drought-sensitive
454 species, which utilizes the richness of hygrophilous life-forms, is proposed. The general
455 procedure and the application of this method are as follows. (1) Investigate the

456 hygrophilous life-form richness in fragmented forests. Based on a previous study
457 (Bates, 1998), candidates for the hygrophilous life-forms are fans, pendants, tall turfs,
458 dendroids, wefts, and large cushions. (2) Apply these results to identify the high-
459 priority fragmented forests for conservation of drought-sensitive species. According to
460 the results using tree models, fragmented forests with high richness of hygrophilous
461 life-forms are identified as being of high-priority for conservation. These forests are
462 expected to maintain forest interior conditions rich in drought-sensitive species. Thus,
463 using this method, one can evaluate the relative importance of fragmented forests for
464 conservation of drought-sensitive species.
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467 As it stands, this method seems to simplify investigations of the richness of drought-
468 sensitive species due to the small number of hygrophilous life-forms. In future studies,
469 improvement of this simplified method should be tested by incorporating a rough
470 indication of the abundance of each life-form, or other indicators.
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474 **4.5. Usefulness and limitations**

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477 Compared to previous studies that use some bryophyte species as indicators for
478 bryophyte conservation (Gignac and Dale, 2005; Stewart and Mallik, 2006), this
479 survey method is more advantageous in conservation studies because of the ubiquity of
480 the life-forms. That is, since bryophyte life-forms do not vary as much between
481 different localities as do species, this method can be applied even if knowledge of the
482 individual bryophyte species is poor. Therefore, this method may help to shed more
483 light on the evaluation of drought-sensitive species for conservation in different
484 regions.

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487 Furthermore, this method seems to be more useful and cost-effective compared to a
488 traditional all-species survey due to the use of life-forms as a basic study unit. Since
489 life-forms are easier to recognize than species, even those who can identify bryophytes
490 to the genus or sometimes family level can recognize them in the field. As for the
491 experts, they can complete this survey very quickly. Recognition may still be hard for

492 those without any training on bryophyte sampling, but it is quite a bit easier to learn
493 how to recognize life-forms than species.
494
495
496 Though this survey method is useful for evaluating drought-sensitive species in
497 relation to moisture availability, the evaluation of this method may not be adequate to
498 precisely measure the site values for bryophyte conservation for the following three
499 reasons. First, when some definite and limited objective, such as rarity, governs the
500 choice of conservation sites, these objectives override the criteria of species richness
501 evaluated by this method. Second, this method cannot evaluate the effects on
502 bryophytes of other environmental factors which may be less related to the life-forms,
503 such as tree species composition (Ojala et al., 2000), air purity (Giordano et al., 2004),
504 past landscape structure (Snäll et al., 2004), and demographic processes (Pereira
505 Alvarenga and Pôrto, 2007; Pharo and Zartman, 2007). Finally, these life-forms
506 represent only one aspect of a wider range of traits characterizing the life strategies of
507 bryophytes (During, 1979; Bates, 1998).
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511 **4.6. Implications for conservation**

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514 Since ecological knowledge of individual bryophyte species is often poor, adequate
515 conservation of most bryophyte species may currently be achieved only through a
516 habitat-based approach (Hallingbäck, 2007). In this respect, this alternative survey
517 method is useful because it can evaluate the forest interior conditions important for
518 drought-sensitive species through life-forms without elaborate measurements.
519 Therefore, this method will provide an important step toward the conservation of the
520 drought-sensitive bryophytes in fragmented forests.

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Appendix

Mosses

Ana for	*Anacamptodon fortunei* Mitt.		Hap mic	*Haplocladium microphyllum* (Hedw.) Broth.	
Ano gig	*Anomodon giraldii* Müll. Hal.		Hap pse	*Haplohymenium pseudo-triste* (Müll. Hal.) Broth.	
Aul jap	*Aulacopilum japonicum* Broth.ex Card.		Hap sie	*Haplohymenium sieboldii* (Dozy & Molk.) Dozy & Molk.	
Bra nep	*Brachymenium nepalense* Hook.		Hap tri	*Haplohymenium triste* (Ces.) Kindb.	
Bra buc	*Brachythecium buchananii* (Hook.) A.Jaeger		Hed cil	*Hedwigia ciliata* (Hedw.) P.Beauv.	
Bra plu	*Brachythecium plumosum* (Hedw.) Schimp.		Her toc	*Herpetineuron toccoae* (Sull. & Lesq.) Card.	
Bra pop	*Brachythecium populeum* (Hedw.) Schimp.		Hyp api	*Hypnodontopsis apiculata* Z.Iwats.& Nog.	
Bra sp.	*Brachythecium* sp.		Hyp mim	*Hypnum plumaeforme* Wilson var.*minus* Broth. ex Ando	
Bro lea	*Brothera leana* (Sull.) Müll. Hal.		Hyp plu	*Hypnum plumaeforme* Wilson var. *plumaeforme*	
Bro fau	*Brotherella fauriei* (Card.) Broth.		Les pus	*Leskeella pusilla* (Mitt.) Nog.	
Bro hen	*Brotherella henonii* (Duby) M.Fleisch.		Leu bow	*Leucobryum bowringii* Mitt.	
Bry nov	*Bryhnia novae-angliae* (Sull. & Lesq.) Grout		Leu jun	*Leucobryum juniperoideum* (Brid.) Müll. Hal.	
Bry arg	*Bryum argenteum* Hedw.		Mac jap	*Macromitrium japonicum* Dozy & Molk.	
Bry cap	*Bryum capillare* Hedw.		Nec hum	*Neckera humilis* Mitt.	
Cal hal	*Callicladium haldanianum* (Grev.) H.A.Crum		Oka bra	*Okamuraea brachydictyon* (Card.) Nog.	
Cam ger	*Campylopus gemmiparus* Z. Iwats.		Oka hak	*Okamuraea hakoniensis* (Mitt.) Broth.	
Cam umb	*Campylopus umbellatus* (Arn.) Paris		Ort con	*Orthotrichum consobrinum* Card.	
Che rhy	*Chenia rhizophylla* (Sakurai) R.H.Zander		Ort erb	*Orthotrichum erubescens* Müll. Hal.	
Dic den	*Dicranodontium denudatum* (Brid.) E. G. Britt. ex Williams		Pal les	*Palamocladium leskeoides* (Hook.) E.G.Britton	
Dru sin	*Drummondia sinensis* Müll. Hal.		Pla act	*Plagiomnium acutum* (Lindb.) T.J.Kop.	
Ent cha	*Entodon challengeri* (Paris) Card.		Pla eur	*Plagiothecium euryphyllum* (Card. & Thér.)Z.Iwats.	
Ent fla	*Entodon flavescens* (Hook.) A.Jaeger		Pla neo	*Plagiothecium nemorale* (Mitt.) A. Jaeger	
Ent sul	*Entodon sullivantii* (Müll. Hal.) Lindb.		Pla rep	*Platygyrium repens* (Brid.) Bruch & Schimp.	
Eur sav	*Eurhynchium savatieri* Schimp.ex Besch.		Pse poh	*Pseudotaxiphyllum pohliaecarpum* (Sull. Lesq.) Z.Iwats.	
Eur lep	*Eurohypnum leptothallum* (Müll. Hal.) Ando		Pyl ten	*Pylaisiadelpha tenuirostris* (Bruch & Schimp.) W.R.Buck	
Fab mat	*Fabronia matsumurae* Besch.		Rhy inc	*Rhynchostegium inclinatum* (Mitt.) A.Jaeger	
Fau ten	*Fauriella tenuis* (Mitt.) Card.		Rhy pal	*Rhynchostegium pallidifolium* (Mitt.) A.Jaeger	
Fis dub	*Fissidens dubius* P.Beauv.		Sch mat	*Schwetschkea matsumurae* Besch.	
For sp.	*Forsstroemia* sp.		Sem sub	*Sematophyllum subhumile* (Müll. Hal.) M.Fleisch.	
Gly hum	*Glyphomitrium humillimum* (Mitt.) Card.				
Gri pil	*Grimmia pilifera* P.Beauv.				
Hap ang	*Haplocladium angustifolium* (Hampe & Müll.Hal.) Broth.				

Appendix (Continued)

Syr jap	*Syrrhopodon japonicus* (Besch.) Broth.		Ulo cri	*Ulota crispa* (Hedw.) Brid.	
Thu kan	*Thuidium kanedae* Sakurai		Ulo jap	*Ulota japonica* (Sull. & Lesq.) Mitt.	
Tor pag	*Tortula pagorum* (Milde) De Not.		Ven sin	*Venturiella sinensis* (Vent.) Müll. Hal.	
Tra mic	*Trachycystis microphylla* (Dozy & Molk.) Lindb.				

Liverworts

Acr pus	*Acrolejeunea pusilla* (Steph.) Grolle & Gradst.		Fru osu	*Frullania osumiensis* (S. Hatt.) S.Hatt.	
Baz jap	*Bazzania japonica* (Sande Lac.) Lindb.		Fru par	*Frullania parvistipula* Steph.	
Baz pom	*Bazzania pompeana* (Sande Lac.) Mitt.		Fur ped	*Frullania pedicellata* Steph.	
Baz tri	*Bazzania tridens* (Reinw.,Blume & Nees) Trevis.		Fru tam	*Frullania tamarisci* (L.)Dumort. subsp. *obscura* (Verd.) S.Hatt.	
Cep spi	*Cephaloziella spinicaulis* Douin		Het pla	*Heteroscyphus planus* (Mitt.) Schiffn.	
Chi min	*Chiloscyphus minor* (Nees) J.J.Engel & R.M.Schust.		Lej jap	*Lejeunea japonica* Mitt.	
			Lej uli	*Lejeunea ulicina* (Tayl.) Gottsche, Lindenb.& Nees	
Col jap	*Cololejeunea japonica* (Schiffn.) S.Hatt. ex Mizut.		Mac ulo	*Macvicaria ulophylla* (Steph.) S.Hatt.	
			Met dec	*Metzgeria decipiens* (C.Massal.) Schiffn.	
Col mim	*Cololejeunea minutissima* (Sm.) Schiffn.		Met lin	*Metzgeria lindbergii* Schiffn.	
Col nak	*Cololejeunea nakajimae* S.Hatt.		Met tem	*Metzgeria temperata* Kuwah.	
Col rad	*Cololejeunea raduliloba* Steph.		Odo sp.	*Odontoschisma* sp.	
Fru div	*Frullania diversitexta* Steph.		Pla sci	*Plagiochila sciophila* Nees ex Lindenb.	
Fru eri	*Frullania ericoides* (Nees) Mont.		Rad con	*Radula constricta* Steph.	
Fru ham	*Frullania hamatiloba* Steph.		Rad jap	*Radula japonica* Gottsche ex Steph.	
Fru inf	*Frullania inflata* Gottsche		Tro san	*Trocholejeunea sandvicensis* (Gottsche) Mizut.	
Fru mus	*Frullania muscicola* Steph.				

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Captions, tables and figures

Table 1

Epiphytic bryophyte species and life-forms records in 27 fragmented forests in Kyoto (Japan). Each column represents presence (+) /absence (blank) of the species. Species richness and life-form richness are shown at the end of the list. The site number is for reference to Fig. 1, and abbreviations of species names for the Appendix. The abbreviation of bryophyte life forms are as follows: t = short turfs, T = tall turfs, cu = small cushions, Cu = large cushions, D = dendroids , Rm = rough mats, Sm=smooth mats, Tl = thread-like forms, Th = thalloid mats, F = fans, W = wefts

Table 2

Comparison of epiphytic bryophyte species richness (mean ± SD) between terminal nodes (Node A-H) resulting from tree models. Nodes A-F resulted from the tree model based on life-forms, and Nodes G-H from the tree model based on environmental conditions (see Fig. 2).

718

719

720 **Fig. 1**

721 Study sites in Kyoto City. Numerals on the map (1-27) show study site locations.

722 Site numbers were assigned in descending order of patch size.

723

724

725 **Fig. 2**

726 Results of the linear models. Results of the linear model based on the life-forms is

727 shown on the top ($y = 6.81x - 11.4$, $R^2 = 0.731$, n =27, $P < 0.01$), and results of the

728 linear model based on environmental conditions on the bottom ($y = 17.1x + 28.1$, $R^2 =$

729 0.661, n =27, $P < 0.01$). In the former model, only life-form richness was selected as a

730 significant explanatory variable, while in the latter, only patch size (logarithmically

731 transformed) was selected from 10 types of candidate variables.

732

733

734 **Fig. 3**

735 Results of tree models. The tree model based on life-forms is shown on the top
736 (proportional reduction in deviance = 0.817), and the tree model based on
737 environmental conditions is on the bottom (proportional reduction in deviance = 0.617).
738 Graphic images of bryophyte life-forms are also presented in the tree model on the top.
739 Bold numerals refer to mean epiphytic bryophyte species richness in the terminal
740 nodes (see Table 2).
741
742
743
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751
752

Table 1

Species	Life-form	Site number																										
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Mosses																												
Ana for	Sm					+				+																		
Ano gig	D/Rm				+	+																						
Aul jap	Tl				+																							
Bra nep	t	+	+		+			+	+					+	+	+	+										+	
Bra buc	Rm				+	+																						
Bra plu	Rm	+	+	+	+	+		+	+			+	+		+	+				+		+					+	
Bra pop	Rm				+			+	+							+						+					+	
Bra sp.	Rm		+											+														
Bro lea	t	+	+	+	+	+		+	+					+	+				+	+			+					
Bro fau	Sm	+	+	+	+		+	+	+	+		+	+		+	+			+			+						
Bro hen	Sm	+	+	+		+	+	+	+	+	+		+	+				+				+	+	+	+			
Bry nov	W					+																						
Bry arg	t			+					+					+						+		+						
Bry cap	cu	+	+	+	+	+	+	+	+			+		+		+										+	+	
Cal hal	Sm				+			+																				
Cam gem	t					+																						
Cam umb	t/T			+					+																			
Che rhy	t								+								+											
Dic den	t		+		+	+	+	+			+																	
Dru sin	Rm	+						+	+				+		+	+										+		
Ent cha	Sm	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+
Ent fla	Sm	+						+								+												
Ent sul	Sm				+							+																
Eur sav	Sm	+		+	+			+	+	+		+		+	+		+		+	+	+	+					+	
Eur lep	Sm	+																										
Fab mat	Tl	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+		+		+	+	
Fau ten	Tl			+	+		+			+	+																	
Fis dub	t						+																					
For sp.	D									+																		
Gly hum	cu	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	
Gri pil	cu					+			+																			
Hap ang	Tl	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+	+		+	+		+		+	+	
Hap mic	Tl	+	+		+															+								
Hap pse	Tl	+	+	+	+	+	+	+	+	+		+			+	+	+	+	+	+		+				+	+	+
Hap sie	Tl		+		+	+						+			+	+						+		+				
Hap tri	Tl	+	+	+	+				+			+							+	+		+					+	
Hed cil	cu/Cu								+			+			+	+												
Her toc	Rm	+	+		+	+		+	+			+	+		+	+	+		+	+	+					+	+	
Hyp api	t			+	+																							
Hyp mim	Rm	+	+	+	+	+	+	+	+		+		+		+	+				+		+	+					
Hyp plu	Rm/W	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+			+		+	
Les pus	Tl	+	+			+							+	+							+							
Leu bow	cu									+																		
Leu jun	cu/Cu	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+		+	+	+		+				
Mac jap	Rm		+		+	+														+							+	
Nec hum	F		+	+	+	+	+				+	+																
Oka bra	Rm	+			+	+	+		+	+		+	+		+	+	+	+	+	+		+				+	+	
Oka hak	Rm	+			+	+		+	+			+			+	+	+					+						
Ort con	cu	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+
Ort erb	cu	+				+									+	+												
Pal les	Rm					+																						
Pla act	W	+	+			+			+																		+	
Pla eur	Sm		+			+	+							+														

Table 1 (continued)

Species	Life-form	Site number																										
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Pla neo	Sm				+														+									
Pla rep	Sm	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+		+		+			+		+	+	
Pse poh	Sm					+	+			+	+													+	+			
Pyl ten	Sm	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+
Rhy inc	Sm	+	+	+	+	+	+	+									+		+		+			+		+	+	
Rhy pal	Sm	+	+	+	+	+	+				+	+	+			+					+	+					
Sch mat	Sm				+								+			+												
Sem sub	Rm	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+			+	+	+	+		+			
Syr jap	t						+																					
Thu kan	W	+				+	+															+						
Tor pag	t	+		+				+						+					+									
Tra mic	Rm/W	+	+	+	+	+		+	+			+							+	+							+	
Ulo cri	cu	+	+	+		+	+			+						+		+				+						
Ulo jap	cu							+			+											+						
Ven sin	Tl	+	+	+	+	+		+	+			+	+	+	+	+	+		+	+	+	+		+			+	
Liverworts																												
Acr pus	Tl	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+
Baz jap	Sm							+																				
Baz pom	Sm					+	+																					
Baz tri	Sm		+				+			+	+							+										
Cep spi	Tl		+			+	+		+										+									
Chi min	Sm	+	+	+	+	+	+	+		+	+	+	+		+	+		+	+		+	+	+	+	+		+	
Col jap	Tl	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+				+	+		+	+
Col mim	Tl		+		+	+																+		+				
Col nak	Tl				+							+																
Col rad	Tl		+		+	+				+	+	+				+			+									
Fru div	Sm			+																								
Fru eri	Sm	+	+		+	+	+		+		+	+	+	+	+	+	+		+			+		+				+
Fru ham	Sm				+	+	+					+										+						
Fru inf	Sm	+				+												+				+						
Fru mus	Sm	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+		+		+	+	+	+	
Fru osu	Sm					+										+												
Fru par	Tl	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+
Fur ped	Sm					+																						
Fru tam	Sm					+																						
Het pla	Sm		+	+		+	+	+	+						+													
Lej jap	Sm	+	+		+				+			+	+														+	
Lej uli	Tl	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+				+
Mac ulo	Sm	+	+	+	+	+	+	+	+	+	+	+	+				+		+	+		+		+				
Met dec	Th		+	+		+	+																	+				
Met lin	Th	+	+	+	+	+	+		+		+	+	+						+									
Met tem	Th						+			+								+										
Odo sp.	Tl					+																						
Pla sci	F						+																					
Rad con	Sm	+			+		+			+		+	+						+	+								
Rad jap	Sm		+				+												+									
Tro san	Sm	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+	+	+	+	+
Species richness		50	52	42	57	63	47	41	45	30	28	41	33	27	33	38	24	19	33	29	19	37	12	24	11	16	29	10
Life-form richness		7	9	9	9	9	8	6	9	7	8	8	6	6	7	7	6	6	7	6	4	6	5	4	4	4	6	3

Table 2

Node	Sample size	Species richness
A	2	60.0 ± 4.2
B	5	42.0 ± 9.0
C	3	42.7 ± 8.7
D	8	32.3 ± 6.0
E	4	23.1 ± 10.1
F	5	16.2 ± 5.6
G	8	49.6 ± 7.6
H	19	25.9 ± 9.3

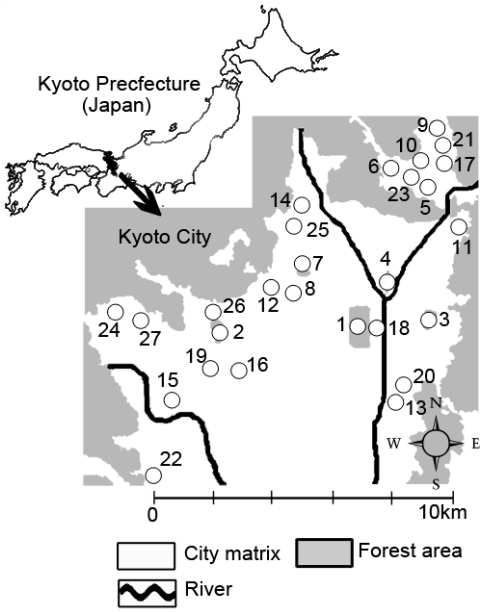


Fig. 1

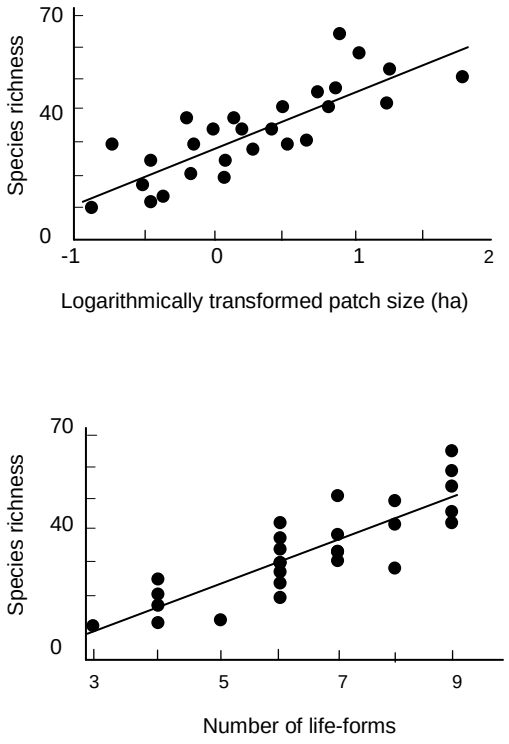
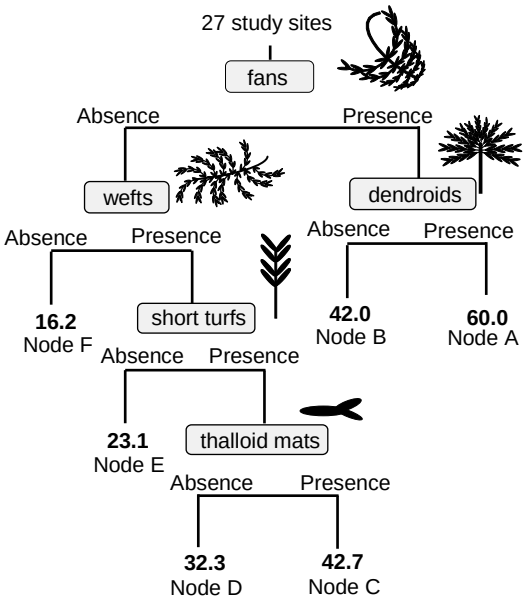


Fig. 2



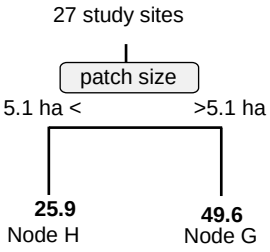


Fig. 3